JHR 28: 37–65 (2012)
doi: 10.3897/JHR.28.3514
www.pensoft.net/journals/jhr

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

The Vespinae of North America (Vespidae, Hymenoptera)

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Academic editor: *Wojciech Pulawski* | Received 12 June 2012 | Accepted 30 July 2012 | Published 24 August 2012

Citation: Kimsey LS, Carpenter JM (2012) The Vespinae of North America (Vespidae, Hymenoptera). Journal of Hymenoptera Research 28: 37–65. doi: 10.3897/JHR.28.3514

Abstract

The species of paper wasps in the tribe Vespini, family Vespidae from America North of Mexico are reviewed, including a new identification key to the genera and species, complete synonymy, distribution and biology. This fauna includes six species of *Dolichovespula* Rohwer, three species of *Vespa* Linnaeus and 13 species of *Vespula* Thomson. No Holarctic species are recognized, with the result that *Dolichovespula arctica* (Rohwer) and Vespula *intermedia* (du Buysson) are again recognized as species, while *Vespula infernalis* (de Saussure) is given new status as a species.

Keywords

Vespa, *Dolichovespula*, *Vespula*

Introduction

Vespinae, or the yellow jackets and hornets, are among the most recognizable wasps in North America. All of the species are either social or are social parasites of other congeners. They construct their nests out of a mixture of plant fibers and salivary secretions, and the nests can range from baseball-sized, with a few thousand cells, to nests with hundreds of thousands of cells. Nests are generally annual but a few species will develop large perennial nests in warm climates. A number of species, such as *Vespula alascensis* and *Vespula germanica*, are considered to be pests because of their willingness

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to build nests in structures and to scavenge a variety of food materials other than live insects, which brings them into frequent contact with humans and because the majority of sting-caused deaths are attributable to yellow jackets.

There have been a number of changes in the North American social vespine fauna since the widely used key published by Akre et al. (1981). Two exotic *Vespa affinis* Linnaeus and *simillima* (Smith) have been introduced into North America. One new species has been described, *Dolichovespula alpicola* Eck (Eck, 1984). In addition, there have been a number of other taxonomic changes based on reevaluation of specimens and study of male genitalia. The most notable of these is the discovery that two species previously considered Holarctic are not in fact found in both North America and the Palearctic. *Vespula vulgaris* (Linnaeus) and *Dolichovespula norwegica* (Fabricius) are not conspecific with the species in North America, necessitating name changes for these taxa (Carpenter et al. 2011, Carpenter and Glare 2010): *Vespula alascensis* (Packard) and *Dolichovespula albida* (Sladen) are valid species. There are morphological differences now known between North American and Eurasian specimens of another supposed Holarctic species, *Vespula austriaca*, and the North American species should therefore be known as *Vespula infernalis* (de Saussure). Another of the supposed Holarctic species, *Dolichovespula adulterina* (du Buysson) is a social parasite, which does not have the same hosts in Eurasia and North America, hence is probably not conspecific in the Old World and New, and *D. arctica* (Rohwer) should be treated as a species. Most likely no Holarctic species should be recognized, with the exception of the introduced *Vespula germanica*, therefore *Vespula intermedia* (du Buysson) should be used instead of *V. rufa* (Linnaeus).

Given these changes, and the difficulty of using many of the existing keys, which rely heavily on coloration, we have developed a new key incorporating these taxonomic changes and attempting to place more emphasis on structural features, such as male genitalia. The key by Akre et al. (1981) was also incomplete, not including socially parasitic species, as it was based only on workers. The key below includes all species and castes.

Materials and methods

North America as construed here is America north of Mexico. Thus two species recently described from central Mexico (*Vespula inexspectata* Eck; Eck 1994) and Guatemala (*V. akrei* Landolt; Landolt et al. 2010) are not included in the key, nor is *Vespa orientalis* Linnaeus, recently recorded from Mexico (Dvořák 2006).

Specimens used in the development of this key were from the collections of the American Museum of Natural History, New York; Bohart Museum of Entomology, University of California, Davis; California State Collection of Arthropods, California

Department of Food & Agriculture, Sacramento, and the U. S. National Museum of Natural History, Washington, D. C.

Type repositories listed in the synonymies include: BUDAPEST – Hungarian Natural History Museum, Budapest; CAMBRIDGE – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; COPENHAGEN – Zoologisk Museum, Universitetsparken, Copenhagen, Denmark; DRESDEN – Staatliches Museum für Tierkunde, Dresden, Germany; GAINESVILLE – Florida State Collection of Arthropods, Gainesville, USA; GENEVA – Museum of Natural History, Geneva, Switzerland; GENOA – Museo Civico di Storia Naturale "Giacomo Doria", Génova, Italy; LEIDEN – Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; LINNAEAN SOCIETY – Linnaean Society, London, UK; LONDON – The Museum of Natural History, London, UK; OTTAWA – Canadian National Collection of Insects, Agriculture Canada, Ottawa; OXFORD – Hope Entomological Collections, Oxford University, England; PARIS – Muséum National d'Histoire Naturelle, Paris, France; PHILADELPHIA – Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; ST. PETERSBURG – Zoological Institute, St. Petersburg, Russia; STOCKHOLM – Naturhistoriska Riksmuseet, Stockholm, Sweden; TAICHUNG – National Museum of Natural Sciences, Taichung, Taiwan; TURIN – Instituto di Zoologia Sistematica, Universita di Torino, Turin, Italy; UPPSALA – Uppsala University Zoological Museum, Uppsala, Sweden; WASHINGTON - U. S. Museum of Natural History, Washington, D. C., USA.

Key to the Yellow Jackets and Hornets of North America

1 Head in dorsal view greatly expanded behind eyes, postocular distance more than twice as broad as distance between hindocelli (as in Fig. 5); *Vespa* Linnaeus **2**

– Head in dorsal view not expanded behind eyes, postocular distance subequal to distance between hindocelli (as in Figs 6, 7)..... **4**

2 Metasomal segments I and II orange or red, posterior segments black, without sublateral free or connected blackish spots (Fig. 26); metapleural punctures ventrally well-defined, nearly contiguous; southern California? .... ***Vespa affinis* (Linnaeus)**

– Metasomal segments basally blackish to brown and apically yellow; metapleural punctures ventrally shallow, separated by 1 puncture diameter or more **3**

3 Female clypeal punctures clearly defined, contiguous or nearly so; male metasomal sterna VI-VII apicomedial margin straight or shallowly indented; metasomal terga III–VI transverse basal black band with sublateral free or connected black spot (Fig. 27); eastern United States..... ***Vespa crabro* Linnaeus**

– Female clypeal punctures medially, shallow, separated by 1 puncture diameter or more; male metasomal sterna VI-VII apicomedial margin deeply emarginate; metasomal terga III transverse basal black band simple, barely undulating (Fig. 28); British Columbia? ..... ***Vespa simillima* (Smith)**

4 Malar space long, one fifth eye height or longer (Figs 2, 9); pronotum with transverse anterodorsal carina; *Dolichovespula* Rohwer **5**

– Malar space short, one-tenth eye height (Figs 4, 10); pronotum without transverse anterodorsal carina; *Vespula* Thomson..... **10**

5 Metasomal terga I-III entirely black (Fig. 33); pronotal lateral angle finely rugose; widespread..... ***Dolichovespula maculata* (Linnaeus)**

– Metasomal terga I-III with pale markings; pronotal lateral angle not rugose 6

6 Occipital carina absent; female clypeal apical margin acutely angulate; male apical flagellomeres without tyloids; Alaska to Newfoundland, south to Arizona, North Carolina, Georgia.....***Dolichovespula arctica* (Rohwer)**

– Occipital carina present; female clypeal apical margin with obtuse to right angles; male apical flagellomeres with tyloids **7**

7 Body, particularly face, with whitish markings, metasomal terga I-II often with lateral red spots (Fig. 29); Alaska, Maine and northern Canada .... ***Dolichovespula albida* (Sladen)**

– Body, particularly face, with yellow markings, usually without red metasomal spots; more southern distribution **8**

8 Metasomal terga I and II broad yellow bands expanded medially into sharp, triangular projection (Fig. 32); genal band continuous, less commonly medially broken; widespread species ..... ***Dolichovespula arenaria* (Fabricius)**

– Metasomal terga I and II with narrow, parallel-sided yellow bands, sometimes slightly narrowed medially; genal band integrity variable **9**

9 Malar space length one-fourth eye height; clypeal apex width 1.5–1.6× malar space length; male apical flagellomeres with two tyloids; Alaska to Newfoundland, south to Colorado, Georgia *Dolichovespula norvegicoides* (Sladen)

– Malar space length one-fifth eye height; clypeal apex width 1.9–2.0× malar space length; male apical flagellomeres with one or two tyloids; western North America, Alaska and Alberta south to Arizona .... ***Dolichovespula alpicola* Eck**

10 Female; six metasomal segments; 10 flagellomeres **11**

– Male, seven metasomal segments; 11 flagellomeres **23**

11 Scutum with two fully developed longitudinal yellow stripes (as in Fig. 11); metasomal sterna I-V with few if any black markings..... **12**

– Scutum without stripes, if stripes present only partly developed; metasomal sterna with extensive black markings..... **13**

12 Metasomal terga II-IV with small oval sublateral black spots (Fig. 46); supraantennal black mark as broad or broader than antennal socket (Fig. 24); primarily from California, with small populations in Arizona, Nevada, Oregon and Baja California, Mexico ..... ***Vespula sulphurea* (de Saussure)**

– Metasomal terga II-IV without small oval sublateral black spots (Fig. 45); supraantennal black mark narrower thanantennal socket (Fig. 25); mostly east of 100th meridian but extending through Texas to Guatemala ..... ***Vespula squamosa* (Drury)**

13 Pale body markings whitish; metasomal tergum II pale apical band narrow and parallel-sided (as in Figs 38, 42) **14**

– Body markings yellow; metasomal tergum II pale apical band usually broad and sinuous or emarginated medially (as in Figs 41, 43) **15**

14 Metasomal terga I and II with reddish markings, tergum I extensively red, with posterior whitish band along apical margin, usually with partial transverse whitish band at apex of anterior face (Fig. 42); Alaska to Newfoundland, south to Vermont ..... ***Vespula intermedia* (du Buysson)**

– Metasomal terga I and II without reddish markings; tergum I black, with partial white band along posterior margin and often partial white band at apex of anterior face (Fig. 38); Canada and northern United States, south to Colorado and Georgia ..... ***Vespula consobrina* (de Saussure)**

15 Eye dorsally margined by continuous yellow band (Figs 10, 23), sometimes narrowly broken; metasomal tergum I with diamond-shaped medial black mark ..... ***Vespula pensylvanica* (de Saussure)**

– Eye not dorsally margined by yellow band on (as in Figs 15, 16), metasomal tergum I with or without diamond-shaped medial black mark..... **16**

16 Hindtibia with long black setae; clypeal apical angles acute in females (Fig. 20); northern North America, south to Arizona, New Jersey ..... ***Vespula infernalis* (de Saussure) stat. n.**

– Hindtibia without long black setae; clypeal apical angles blunt in females (as in Fig. 16) **17**

17 Scape yellow ventrally **18**

– Scape without yellow ventrally, although may be dark brown ventrally **20**

18 Metasomal tergum II largely black, irregularly parallel-sided, with narrow apical yellow band and without sublateral yellow spot or spot faint (Fig. 47); northeastern North America south to Georgia and Alabama, west to Iowa.... ..... ***Vespula vidua* (de Saussure)**

– Metasomal tergum II black band apically lobate, with broad apical yellow band as broad or broader than apical bands on III-V, and usually with sublateral yellow spot (as in Figs 35, 37) **19**

19 Metasomal tergum II black band angulate medially; gena with continuous yellow band in side view, sometimes interrupted by black spot or narrow medial interruption (Fig. 37) ..... ***Vespula atropilosa* (Sladen)**

– Metasomal tergum II black band broadly rounded medially, often having free lateral yellow spots; gena with yellow band broadly interrupted by black spot, rarely continuous (Fig. 35) ..... ***Vespula acadica* (Sladen)**

20 Supraantennal black band as broad or broader than antennal socket; gena with yellow band broadly interrupted by black spot in side view..... ..... ***Vespula alascensis*** **(Packard)**

– Supraantennal black band much narrower than antennal socket; gena with yellow band uninterrupted or narrowly broken in side view.....**21**

21 Metasomal tergum I with diamond-shaped or somewhat broader medial black mark, attachment to anterior black band no narrower than one-third of width (Fig. 40)..... ***Vespula germanica*** **(Fabricius)**

– Metasomal tergum I with nearly free broadly diamond-shaped or triangular black mark or black mark broadly attached to anterior band.....**22**

22 Metasomal tergum I with anchor-shaped medial black mark, narrowly connected to anterior black band, if melanistic with at least pair of transverse yellow spots present (Fig. 43)..... ***Vespula maculifrons*** **(Buysson)**

– Metasomal tergum I with triangular medial black mark, broadly connected to anterior black band (Fig. 39)..... ***Vespula flavopilosa*** **Jacobson**

23 Paramere dorsomedial margin evenly convex, without well-developed acute tooth or angle (as in Fig. 78A); volsella without large, densely setose digitus (as in Fig. 78).....**24**

– Paramere dorsomedial margin with well-developed tooth or angle (as in Fig. 80A); volsella with large, densely setose digitus extending nearly as long as aedeagus, visible as dense brush of long setae at apex of genital capsule (as in Fig. 80).....**31**

24 Scutum with two longitudinal yellow stripes (as in Fig. 11).....**25**

– Scutum without longitudinal yellow stripes **26**

25 Aedeagus elongate, strongly exserted beyond apex of paramere by one-half of paramere length or longer (as in Figs 71, 78).... ***Vespula sulphurea*** **(Saussure)**

– Aedeagus short, broad, exserted beyond apex of paramere by one-third of paramere length or less (Figs 70, 77)..... ***Vespula squamosa*** **(Drury)**

26 Body with pale markings whitish **27**

– Body with pale markings yellow.....**28**

27 Basal metasomal segments without red markings (Fig. 38)..... ..... ***Vespula consobrina*** **(de Saussure)**

– Basal metasomal segments with red markings (Fig. 42)..... ..... ***Vespula intermedia*** **(du Buysson)**

28 Metasomal tergum I with diamond-shaped medial black mark, tergum II with broad irregularly lobate posterior yellow band (Fig. 37) .... ***Vespula atropilosa*** **(Sladen)**

– Metasomal terga I and II with narrow subparallel-sided posterior yellow band (as in Fig. 35).....**29**

29 Clypeus with large medial black spot or stripe (Fig. 14)..... ..... ***Vespula acadica*** **(Sladen)**

– Clypeus without single medial black spot or black spot small irregular (as in Fig. 20).....**30**

30 Hindtibia without long black setae; clypeal apical angle obtusely angulate.... ..... ***Vespula vidua*** **(de Saussure)**

– Hindtibia with long black setae (even rubbed specimens have a few); clypeal apical angle blunt but well-developed (Fig. 20)..... ..... ***Vespula infernalis*** **(de Saussure)**

31 Metasomal tergum I with diamond shaped medial black mark narrowly connected to black band (as in Figs 40, 44) **32**

– Metasomal tergum I with parallel-sided black band, black band with triangular medial projection, broadly attached to rest of band (as in Figs 36, 39) **34**

32 Aedeagus without lobe or process behind apex (Fig. 69, 80); eye usually margined by continuous yellow band (as in Fig. 10) or yellow band broken by narrow black line dorsally (may be more broadly interrupted in some males) ..... ***Vespula pensylvanica*** **(Saussure)**

– Aedeagus with short rounded (*germanica,* Fig. 67) or pointed (*maculifrons*, Fig. 68) process behind apex; eye with yellow marginal band always broadly broken dorsally **3**

33 Metasomal tergum VII undulate, rounded dorsally in lateral view (Fig. 13); metasomal terga II-IV with free sublateral black spot or spot narrowly connected to black band (Fig. 40) ..... ***Vespula germanica*** **(Fabricius)**

– Metasomal tergum VII step-like in lateral view, angulate dorsally in lateral view (Fig. 12); metasomal terga II-IV without free or narrowly connected sublateral black spots (Fig. 43), if melanistic with at least pair of transverse yellow spots present ..... ***Vespula maculifrons*** **(du Buysson)**

34 Supraantennal black band much narrower than antennal socket at least medially; metasomal terga II-V with strongly trilobate black band (Fig. 39) .... ***Vespula flavopilosa*** **Jacobson**

– Supraantennal black band as wide or wider than antennal socket; metasomal terga II-V with black band parallel-sided or weakly lobate (Fig. 36)..... ..... ***Vespula alascensis*** **(Packard)**

Taxonomy, biology and distributions

Genus *Dolichovespula* Rohwer

Vespula (*Dolichovespula*) Rohwer 1916:642. Type species: *Vespa maculata* Linnaeus 1763. Original designation.

Pseudovespa (*Pseudovespula*) Bischoff 1931:346. Type species: *Pseudovespa adulterina* Buysson (=*Vespa norwegica* var. *adulterina* du Buysson 1905). Original designation.

Dolichovespula (*Boreovespula*) Blüthgen 1943:149. Type species: V*espa norwegica* Fabricius (=*Vespa norwegica* Fabricius 1781). Original designation.

Dolichovespula (*Metavespula*) Blüthgen 1943:149. Type species: *Vespa silvestris* Scopoli [!] (=*Vespa sylvestris* Scopoli 1763). Original designation.

Dolichovespula albida **(Sladen)**
http://species-id.net/wiki/Dolichovespula_albida
Figs 29, 48

Vespa marginata Kirby 1837:265, pl. VI, fig. 2. Syntype females; New York, latitude 65° (repository unknown). Nec *Vespa marginata* Gmelin 1790.
Vespa albida Sladen 1918:71. Lectotype male; Alaska (OTTAWA).

Distribution. This species occurs in the Hudsonian Zone of North America from Alaska to Maine.

Biology. *Dolichovespula albida* was split again from *D. norwegica* (Fabricius) by Carpenter et al. (2012). The nests are generally small and may be subterranean (Bequaert 1932), although Yamane et al. (1980) reported an aerial nest just above ground.

Dolichovespula alpicola **Eck**
http://species-id.net/wiki/Dolichovespula_alpicola
Figs 30, 49, 54

Dolichovespula alpicola "Wagner" Eck 1984:40 (key), fig. 3L; 1987:191. Lectotype female; USA: Wyoming (DRESDEN).

Distribution. This is a northern boreal species found in western North America from Alaska to Alberta, and extending as far south as Arizona and New Mexico along the Rocky Mountains (R. Jacobson personal communication).

Biology. *Dolichovespula alpicola* is generally found in mixed hardwood-conifer forests in mountainous regions. There is little information on the nesting biology in this species. Eck (1984) attributed the species to Wagner in a key, thus validly publishing it. Eck (1987) later published a fuller description and designated a lectotype.

Dolichovespula arctica **(Rohwer)**
http://species-id.net/wiki/Dolichovespula_arctica
Figs 31, 50, 55

Vespa borealis Lewis 1897:171 (key), 174 [misidentification]. Syntypes (PHILADELPHIA).
Vespula arctica Rohwer 1916:642 (key; in subgenus *Dolichovespula*). Replacement name for *Vespa borealis sensu* Lewis.

Distribution. It occurs as far south as California, Arizona and Georgia in North America. Pale markings can be yellow or whitish in *D. arctica*.

Biology. This species is an obligatory social parasite of *Dolichovespula arenaria* (Wheeler and Taylor 1921) and *D. alpicola* (Wagner 1978). The name is a replacement for a misidentification of *Vespa borealis* Kirby by Lewis (1897), and probably needs to be split from *D. adulterina* (du Buysson), a Palearctic species that has different host species (*D. saxonica* and *D. norwegica*; see Dvořák 2007).

Dolichovespula arenaria **(Fabricius)**

http://species-id.net/wiki/Dolichovespula_arenaria
Figs 32, 51, 56

Vespa arenaria Fabricius 1775:365. Holotype female; "America arenosis" (LONDON).
Vespa borealis Kirby 1837:264. Holotype female; Canada (repository unknown).
Vespa diabolica de Saussure 1854:138. Syntype females; "L'Amerique du Nord, Philadelphia" (TURIN).
Vespa fernaldi Lewis 1897:173. Holotype female; "Colorado" (PHILADELPHIA).

Distribution. This species is abundant throughout boreal North America.

Biology. *Dolichovespula arenaria* feeds on live prey but will occasionally visit carrion. It builds aerial nests, like *D. maculata*, but its nests are usually built in more sheltered sites, such as within bushes, trees, on houses and outbuildings, and rarely even under rocks.

Dolichovespula maculata **(Linnaeus)**

http://species-id.net/wiki/Dolichovespula_maculata
Figs 2, 6, 9, 33, 52, 57

Vespa maculata Linnaeus 1763:412. Lectotype female; "Pensylvania" (STOCKHOLM).
Vespa maculata americana Christ 1791:239. Type destroyed; "mitternachtlichen Amerika". Nec *Vespa americana* Fabricius 1775.

Distribution. The species occurs throughout North America.

Biology. This is the only *Dolichovespula* in North America with the anterior part of the metasoma completely black, and the pale markings are always whitish. It builds aerial nests, which are usually found in exposed places such as hanging from tree branches. These wasps usually feed on live prey, particularly spiders and flies.

***Dolichovespula norvegicoides* (Sladen)**
http://species-id.net/wiki/Dolichovespula_norvegicoides
Figs 34, 53, 58

Vespa norvegicoides Sladen 1918:71. Lectotype female; Amherst, Nova Scotia (OTTAWA).

Distribution. *D. norvegicoides* is relatively rarely collected, although it occurs widely throughout northern North America and further south along mountain ranges.

Biology. This species builds small, aerial nests.

Genus *Vespa* Linnaeus

Vespa Linnaeus, 1758:343, 572. Type species: "*Vespa crabro* Fabricius" (=*Vespa crabro* Linnaeus 1758). Designated by Latreille 1810:438.

Macrovespa Dalla Torre 1904:64, group of genus *Vespa* Linnaeus. Type species: *Vespa crabro* Linnaeus 1758. Designated by Bequaert 1930: 64.

Vespa (*Nyctovespa*) van der Vecht 1959: 210. Type species: *Vespa binghami* du Buysson 1905. Original designation.

***Vespa affinis* (Linnaeus)**
http://species-id.net/wiki/Vespa_affinis
Figs 5, 26

Apis affinis Linnaeus 1764:417. Holotype female; "in Calidus regionibus" (UPPSALA).

Vespa affinis Fabricius 1787:287. Holotype; "in China" (COPENHAGEN). Nec *Vespa affinis* (Linnaeus) 1764.

Vespa unifasciata Olivier 1792:677. Type unknown; "Indes orientales". Nec *Vespa unifasciata* Gmelin 1790.

Vespa alduini Guérin-Méneville 1831:pl. 9 fig. 6; 1838: 264. Holotype; "l'île de Bourou, l'une des Moluques" (Indonesia) (GENOA).

Vespa bimaculata Guérin-Méneville: 264. Unnecessary replacement name for *Vespa alduini* Guérin-Méneville. Nec *Vespa bimaculata* Geoffroy 1785 and *Vespa bimaculata* Olivier, 1792.

Vespa nigripennis de Saussure: 1854:156. Holotype; "Les Philippines" (LONDON). Nec *Vespa nigripennis* Degeer 1773.

Vespa cincta var. *picea* du Buysson 1905 (1904):537. Lectotype female; New Guinea (GENOA).

Vespa indosinensis Pérez 1910:8. Lectotype female; Annam (PARIS).

Vespa formosana Sonan 1927:125. Syntype male, female; Taihoku (Taiwan) (TAICHUNG).

Vespa affinis var. *continentalis* Bequaert 1936:350. Holotype female; India: Mangalore (WASHINGTON).
Vespa affinis var. *hainanensis* Bequaert 1936:347. Holotype female; China: Hainan Island (CAMBRIDGE).
Vespa affinis nigriventris van der Vecht 1957:29. Holotype female; "Palawan" (Philippines) (GAINESVILLE).
Vespa affinis rufonigrans van der Vecht 1957:29. Holotype female; "Palu, Northwest Celebes" (Indonesia) (LIEDEN).
Vespa affinis archboldi van der Vecht 1957:32. Holotype female; "Hollandia" (New Guinea) (LIEDEN).
Vespa affinis moluccana van der Vecht 1957:32. Holotype female, "Saparua I. Near Amboina" (Indonesia) (LIEDEN).
Vespa affinis alticincta van der Vecht 1957:33. Holotype female; New Britain (LONDON).

Distribution. There is a single report of a colony of this Asian species in North America, from San Pedro, in Los Angeles Co., California in 2010 (LSK, personal observation). It is not clear if the species has become established in California. It has also been introduced into New Zealand. Its native range is from India to the Bismarck Islands.

Biology. In Asia, *Vespa affinis* builds large aerial nests of up to several thousand workers (Archer 1997). These wasps are predatory on other insects including honey bees near their hives.

***Vespa crabro* Linnaeus**
http://species-id.net/wiki/Vespa_crabro
Fig. 27

Vespa crabro Linnaeus 1758:572. Holotype female; "in Europae" (LINNAEAN SOCIETY).
Vespa vexator Harris 1776:128. Holotype female; "English" (destroyed).
Vespa crabro major Retzius 1783:63. Type unknown.
? *Vespa pratensis* Geoffroy (*in* Fourcroy) 1785:437. Type unknown; France.
Vespa crabro germana Christ 1791:215. Type unknown (destroyed).
Vespa crabroniformis Smith 1852:40. Syntype male, female; "north China" (LONDON).
Vespa crabro var. *borealis* Radoszkowski 1863:128. Syntype male, female; "Pargolova i Osinovoa Roshchi" (type lost?). Nec *Vespa borealis* Kirby 1837, *Vespa borealis* Zetterstedt 1840 and *Vespa borealis* Smith, 1843.
Vespa crabro var. *anglica* Gribodo 1892:242. Syntype females; "Inghilterra" (GENOA). Nec *Vespa anglica* Smith, 1843.
Vespa oberthuri du Buysson 1902:140. Lectotype female; "Chine: Se-tchouen, Siao-Lou" (China) (PARIS).
Vespa flavofasciata Cameron 1903:280. Holotype female; Japan: Nügata (Shinanogawa) (LONDON).

Vespa crabro var. *tartarea* du Buysson 1905:506. Holotype female; "Japon: Yokohama (BUDAPEST).

Vespa crabro var. *altaica* Pérez 1910:5. Holotype female: "Altai" (PARIS).

Vespa crabro var. *caspica* Pérez 1910:6. Holotype female; "Talysch et Lenkoran, région Caspienne" (Azerbaijan) (PARIS).

Vespa crabro nigra Birula 1925:55. Synypes; West Siberia (ST. PETERSBURG). Nec *Vespa nigra* Geoffroy 1785.

Vespa crabro vulgata Birula 1925:55. Syntypes ?; western Europe (ST. PETERSBURG).

Vespa crabro meridionalis Birula 1925:55. Syntypes ?; western Europe (ST. PETERSBURG).

Vespa crabro chinensis Birula 1925:55. Syntypes ?; middle and south China (ST. PETERSBURG). Nec *Vespa chinensis* Fabricius 1793.

Vespa crabro var. *birulai* Bequaert 1931:105. Replacement name for *Vespa crabro chinensis* Birula.

Vespa crabro var. *gribodoi* Bequaer, 1931:105. Replacement name for *Vespa crabro* var. *anglica* Gribodo.

Distribution. The central European color form of this Palearctic species was introduced into the New York area in the mid-1800's (de Saussure 1898). It now occurs throughout the eastern United States, east of the Mississippi River.

Biology. Nests are generally built in above-ground cavities, wall voids, hollow trees, and even in abandoned honey bee hives. Nests are large in size because of the size of the wasps but generally contain only a few thousand cells. These wasps feed on live insects, including honey bees near hives (Akre and Davis 1978) and have been recorded girdling saplings to feed on sap in the spring (Bromley 1931).

***Vespa simillima* (Smith)**
http://species-id.net/wiki/Vespa_simillima
Figs 3, 8, 28

Vespa simillima Smith 1868:280. Holotype female; Japan: Hakodadi (LONDON).

Vespa mongolica André 1884:lix. Syntype male, female; "Wladivostock, sur l'Amour, dans la Sibérie orientale" (western Russia) (PARIS).

Vespa xanthoptera Cameron 1903:278. Holotype male: Japan: Michzusawa (LONDON).

Vespa micado Cameron 1903:279. Holoytpe female; Japan: Nagasaki (LONDON).

Vespa mongolica var. *sexpunctata* Pérez 1905:79. Holotype female; Japan: Yokohama (PARIS).

Vespa mongolica var. *flavata* Pérez 1910:17. Holotype female; "Chine" (PARIS).

Distribution. This East Asian species was introduced into British Columbia, Canada but has apparently not become established. We have included it in this review because of the potential for a reintroduction.

Biology. Nests are built in a wide variety of situations including in bushes, underground cavities, hollow trees, under eaves, in attics, on rock walls, and in wall voids. As with the other *Vespa* species *affinis* is predatory on other insects, including honey bees.

Genus *Vespula* Thomson

Vespa (*Vespula*) Thomson 1869:79 (8 species). Type species: *Vespa austriaca* Panzer 1799. Designated by Ashmead 1902:164.

Vespa (*Pseudovespa*) Schmiedeknecht 1881:314. Type species: *Vespa austriaca* Panzer 1799, by monotypy.

Dolichovespula (*Paravespula*) Blüthgen 1938:271. Type species: *Vespa vulgaris* Linnaeus 1758. Original designation.

Paravespula (*Allovespula)* Blüthgen 1943:149. Type species: *Paravespula rufa* (Linné) (=*Vespa rufa* Linnaeus 1758), by monotypy.

Vespula (*Rugovespula*) Archer 1982:261, 264. Type species: *Vespa koreensis* Radoszkowski, 1887. Original designation.

Vespula acadica (Sladen)

http://species-id.net/wiki/Vespula_acadica

Figs 14, 35, 59, 72

Vespa rufa var. *americana* du Buysson 1905:592. Holotype male; Canada: Quebec (repository unknown). Nec *Vespa americana* Fabricius 1775, and *Vespa maculata americana* Christ 1791.

Vespa acadica Sladen 1918:72. Lectotype female; Canada: Ottawa (OTTAWA).

Vespula rufa var. *sladeni* Bequaert 1932:102. Holotype female; Washington State (CAMBRIDGE).

Distribution. This is primarily a boreal species, occurring across subArctic Canada and southern Alaska. Its range extends further south in the Rocky, Sierra, Cascade, Siskiyou and Appalachian mountains.

Biology. *Vespula acadica* feeds on live insects and builds small subterranean nests.

Vespula alascensis (Packard)

http://species-id.net/wiki/Vespula_alascensis

Figs 15, 36, 65, 81

Vespa alascensis Packard 1870:27, pl. II fig. 10. Holotype female; "Lower Yukon" (Repository unknown).

Vespa westwoodii Shipp 1893:450. Holotype female; "N. Amer. Bor." (OXFORD).

Distribution. Widespread in North America

Biology. *Vespula alascensis* nests are usually built in subterranean cavities or in structures. The nests can be huge and may become perennial in warmer climates. This species feeds on live prey but will scavenge any source of protein or sugar. It has been introduced into Hawaii, but is not now established (Carpenter 2008, under *vulgaris*).

This North American species was usually known as *Vespula vulgaris* (Linnaeus), based on the similarity between the American and European populations. Carpenter and Glare (2010) discovered that the European and American populations are not conspecific based on features of the male genitalia and mitochondrial DNA evidence.

***Vespula atropilosa* (Sladen)**
http://species-id.net/wiki/Vespula_atropilosa
Figs 16, 37, 60, 73

Vespa atropilosa Sladen 1918:72. Lectotype female; Canada: Lethbridge (OTTAWA).

Distribution. *Vespula atropilosa* occurs in mountain regions from the Rocky Mountains west.

Biology. This species builds subterranean nests, preferring open areas, including pastures and golf courses. It is predatory on other insects.

***Vespula consobrina* (Saussure)**
http://species-id.net/wiki/Vespula_consobrina
Figs 17, 38, 61, 74

Vespa consobrina de Saussure 1854:141. Holotype female; "L'île de Terre-Neuve" (PARIS).
Vespa scelesta McFarland 1888:298. Lectotype female; "Montana" (PHILADELPHIA).

Distribution. *Vespula consobrina* occurs in the Canadian and Transition Zones of northern and central North America.

Biology. This predatory species preys on live insects and usually nests in cavities, using sites in logs, wall voids and rodent burrows.

***Vespula flavopilosa* Jacobson**
http://species-id.net/wiki/Vespula_flavopilosa
Figs 18, 39, 66, 82

Vespula flavopilosa Jacobson (in Jacobson et al.) 1978:303. Holotype female; Ithaca, New York (WASHINGTON).

Distribution. *Vespula flavopilosa* occurs in the eastern United States as far south as Georgia (R. Jacobson, personal communication).

Biology. It builds subterranean nests. This species feeds on live insects, as well as other sources of sugar and protein, and is a scavenger much like *Vespula germanica, V. pensylvanica* and *V. alascensis*.

***Vespula germanica* (Fabricius)**
http://species-id.net/wiki/Vespula_germanica
Figs 1a, b, 13, 19, 40, 67, 83

? *Vespa maculata* Scopoli 1763:312. Type destroyed; "Carnioliae" (Slovenia). Nec *Vespa maculata* Linnaeus 1763.
? *Vespa macularis* Olivier 1792:695. Unjustified emendation of *Vespa maculata* Scopoli.
Vespa germanica Fabricius 1793:256. Type unknown; "Kiliae" (Germany) (repository unknown).

Distribution. *Vespula germanica* has been unintentionally introduced into temperate regions worldwide. It apparently first appeared in Montreal in the 1960's and other parts of eastern North America in the 1970's, although there is a record of the species collected in Ithaca, New York in 1891 (Menke and Snelling 1975). The species reached California by 1989.

Biology. The nests are usually built in structures or less commonly in the ground. Nests can be huge and may become perennial in warmer climates. These wasps feed on live prey or scavenge any source of protein or sugar.

***Vespula infernalis* (de Saussure), stat. n.**
http://species-id.net/wiki/Vespula_infernalis
Figs 4, 7, 20, 41, 62, 75

Vespa infernalis de Saussure 1854:139. Holotype female; "L'Amérique du Nord, Philadelphie (TURIN?).
Vespa tripunctata Packard 1870:26, pl. II fig. 11. Holotype female: "Kutleet", USA (repository unknown). Nec *Vespa tripunctata* Fabricius 1787 and *Vespa tripunctata* Schenck 1861.

Distribution. The distribution of *Vespula austriaca* closely resembles that of *acadica*, occurring in subarctic Alaska and Canada, and southward in the western mountain ranges.

Biology. This is an obligatory social parasite of *Vespula acadica* (Reed et al. 1979). This species has been known as *Vespula austriaca*, a Palearctic species, since Bequaert (1916), but there are sculptural differences in queens between Palearctic and Nearctic specimens.

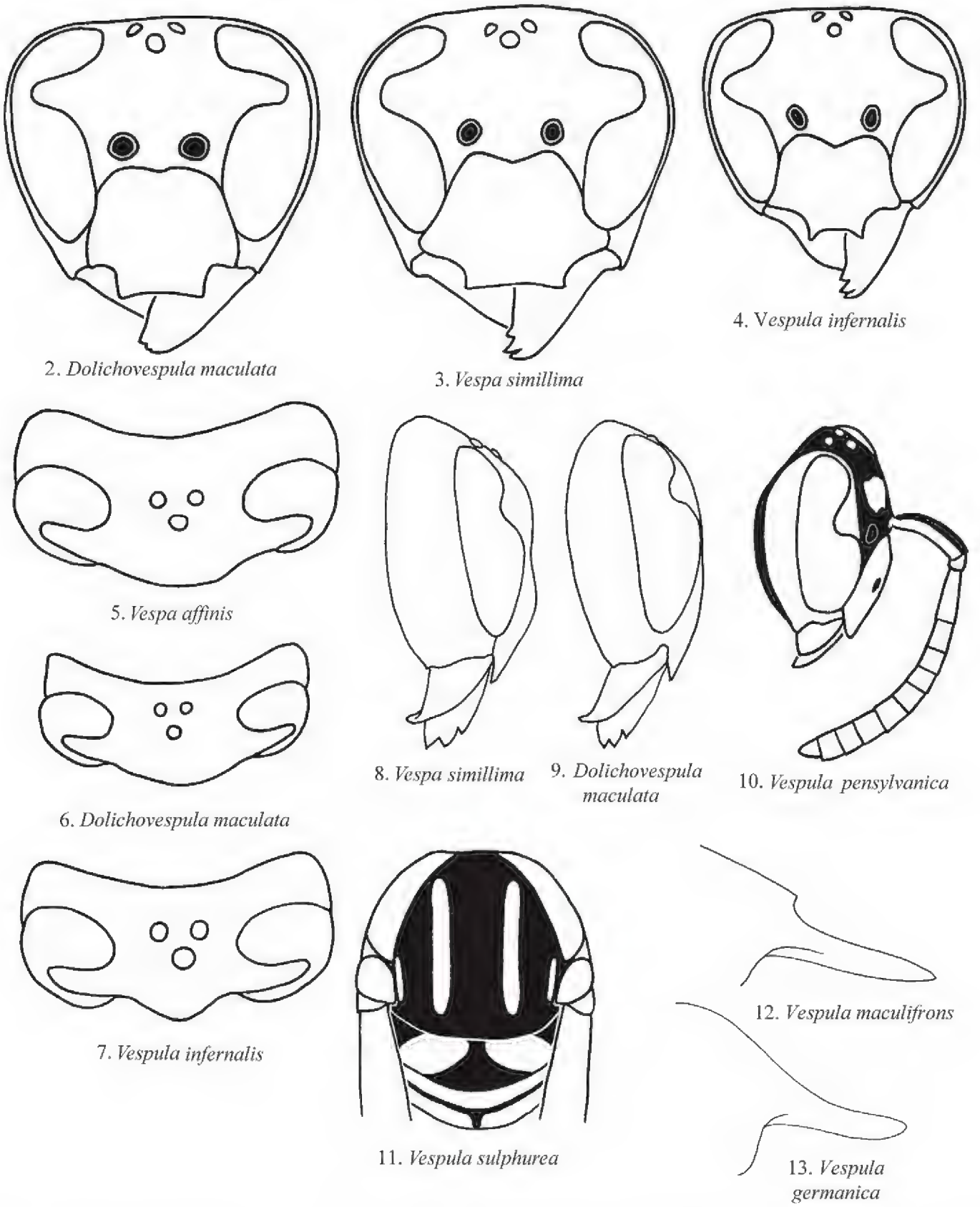
Figure 1. *Vespula germanica* worker **a** side view **b** dorsal view; *Vespula pensylvanica* worker **c** side view **d** dorsal view.

***Vespula intermedia* (du Buysson)**
http://species-id.net/wiki/Vespula_intermedia
Figs 21, 42, 63, 76

Vespa rufa var. *intermedia* du Buysson 1905:591. Syntype male, female; Manchuria, Hudson's Bay (PARIS, LONDON).

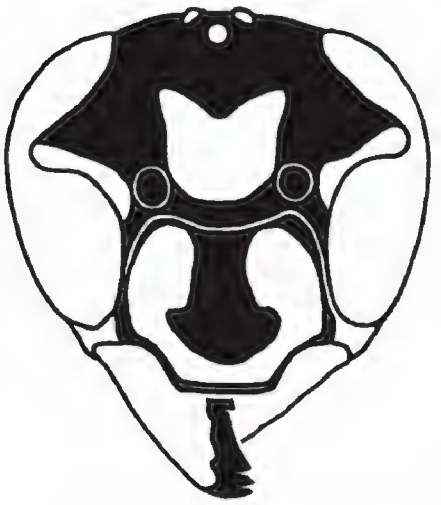
Distribution. These wasps occur in the far northern Nearctic Region.

Biology. The biology of North American *intermedia* has not been studied. *Vespula rufa* in the Palearctic usually nests below ground, in cavities or under eaves. They prey on live insects.

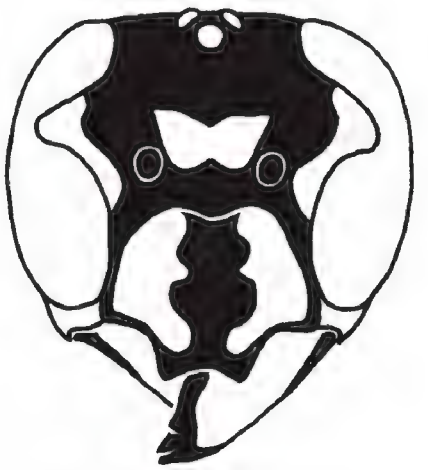


Figures 2–13. 11–12 Front view of face **5–7** Dorsal view of head **8–10** Lateral view of head **11** Dorsal view of thorax **12, 13** Lateral view of male metasomal tergum VII.

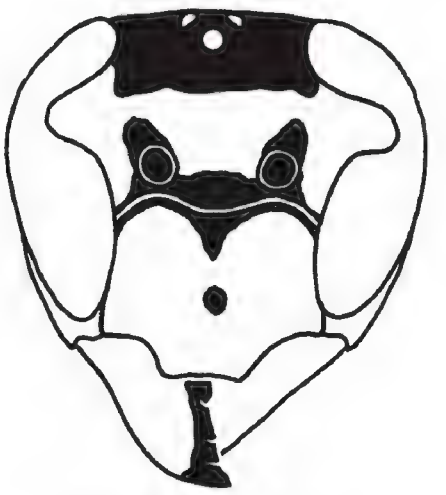
Although treated as a synonym of *Vespula rufa* (Linnaeus), which is thus a Holarctic species, the North American population is probably distinct and should be treated as a separate species, *V. intermedia* (du Buysson). It differs in coloration from *V. rufa*, with the pale markings being whitish and the metasomal terga I-II with reddish markings. The pale markings are either yellow in *V. rufa* (European specimens), or the terga lack reddish markings (Eastern Palearctic), or there are whitish spots in addition to reddish markings (Eastern Palearctic).



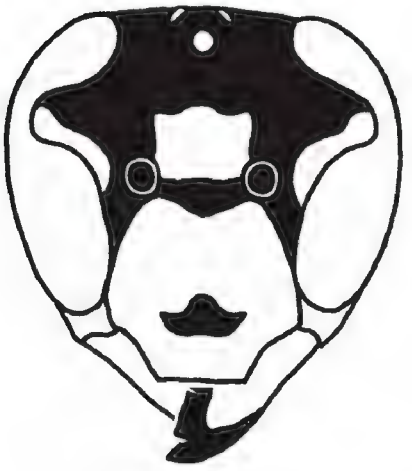
14. *Vpl. acadica*



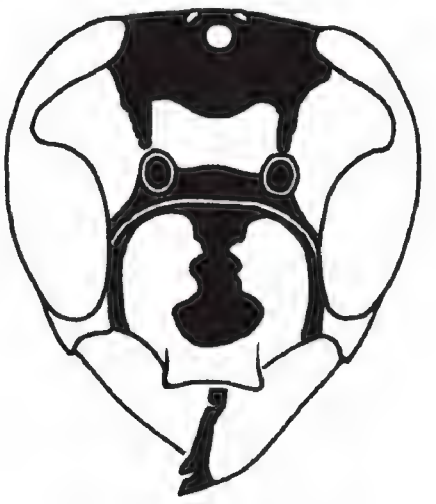
15. *Vpl. alascensis*



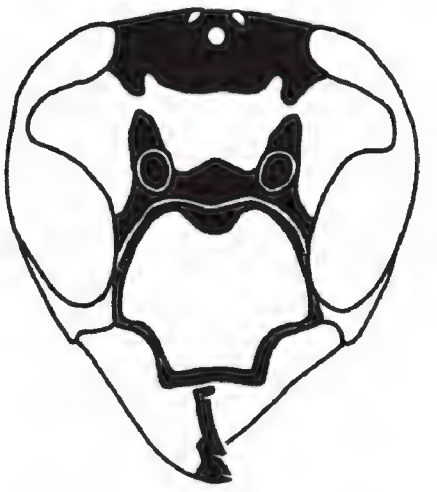
16. *Vpl. atropilosa*



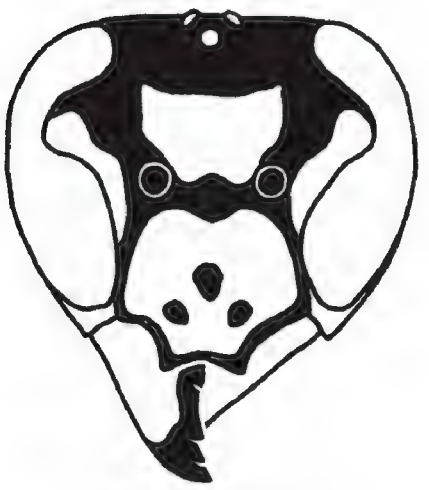
17. *Vpl. consobrina*



18. *Vpl. flavopilosa*

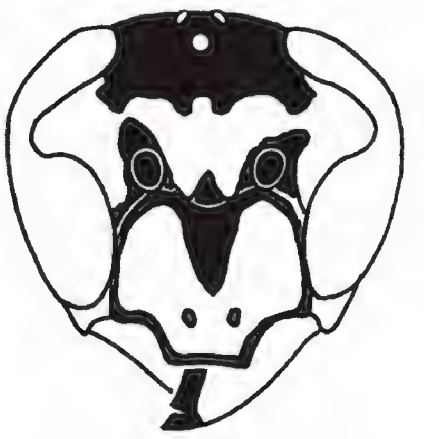


19. *Vpl. germanica*

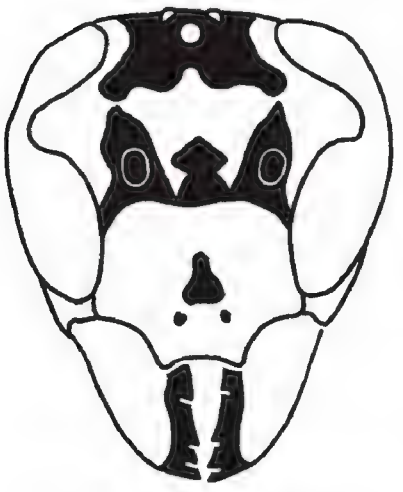


20. *Vpl. infernalis*

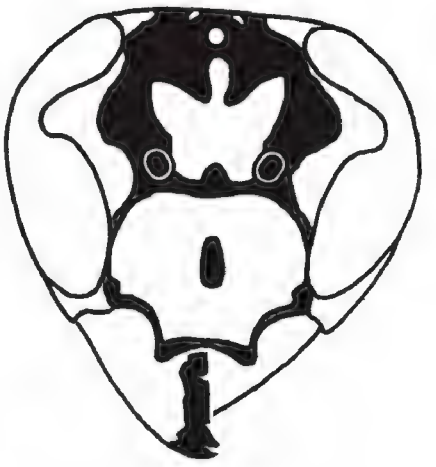
21. *Vpl. intermedia*



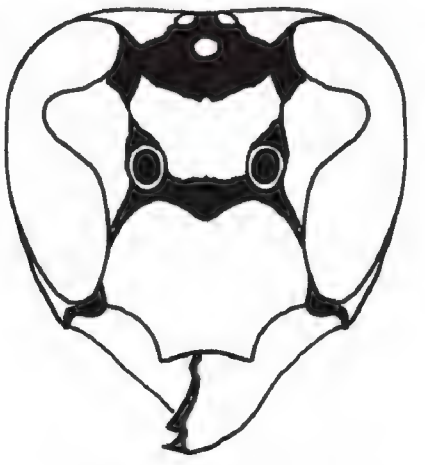
22. *Vpl. maculifrons*



23. *Vpl. pensylvanica*



24. *Vpl. sulphurea*



25. *Vpl. squamosa*

Figures 14–25. Front view of face, antennae removed. *Vpl.* = *Vespula*.

26. *Vespa affinis*

27. *Vespa crabro*

28. *Vespa simillima*

29. *Dolichovespula albida*

30. *Dolichovespula alpicola*

31. *Dolichovespula arctica*

32. *Dolichovespula arenaria*

31. *Dolichovespula maculata*

34. *Dolichovespula norveigicoides*

35. *Vespula acadica*

36. *Vespula alascensis*

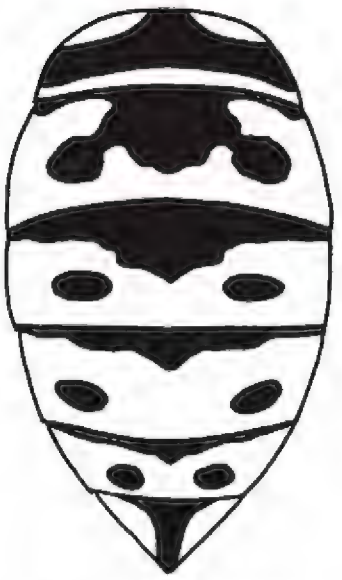
37. *Vespula atropilosa*

Figures 26–37. Dorsal view of worker metasoma.

38. *Vespula consobrina*

39. *Vespula flavopilosa*

40. *Vespula germanica*



41. *Vespula infernalis*

42. *Vespula intermedia*

43. *Vespula maculifrons*

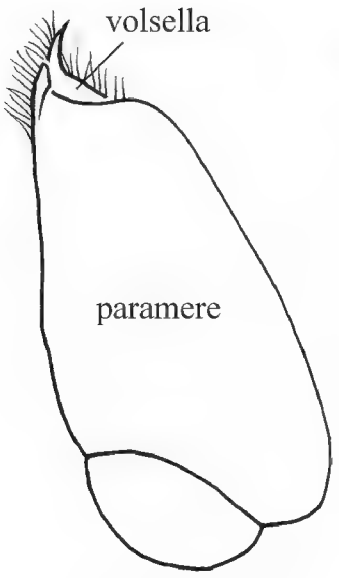
44. *Vespula pensylvanica*

45. *Vespula squamosa*

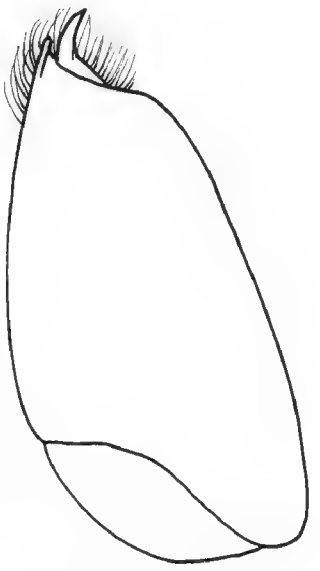
46. *Vespula sulphurea*

47. *Vespula vidua*

Figures 38–47. Dorsal view of worker metasoma.



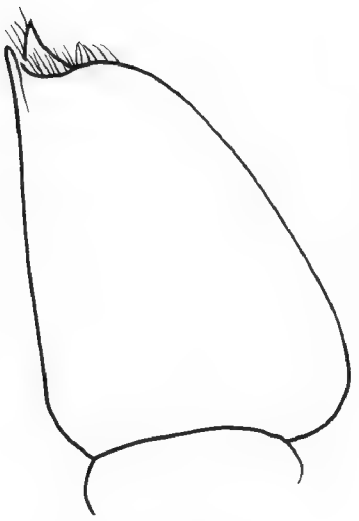
48. *D. albida*



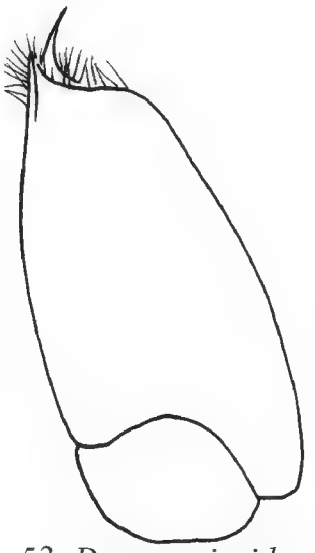
49. *D. alpicola*

50. *D. arctica*

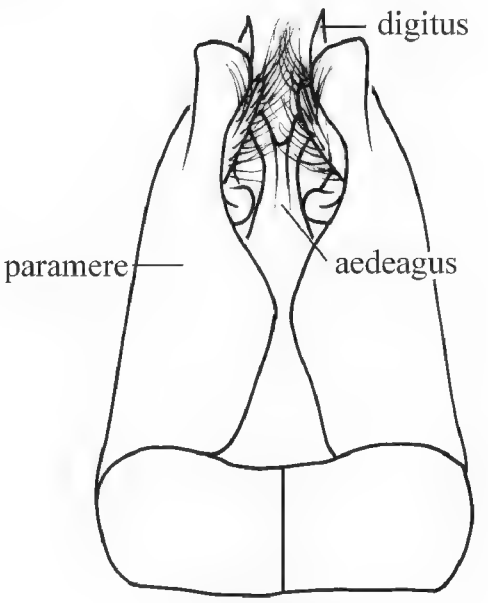
51. *D. arenaria*



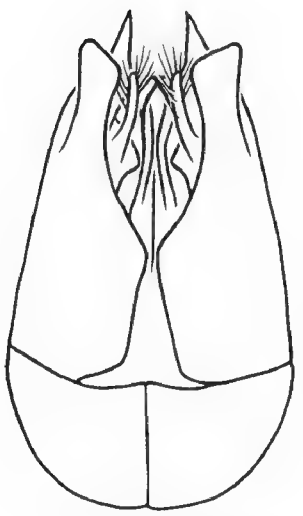
52. *D. maculata*



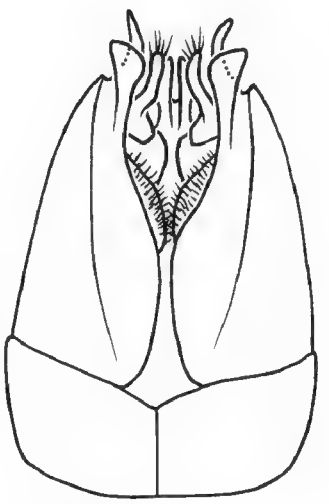
53. *D. norvegicoides*



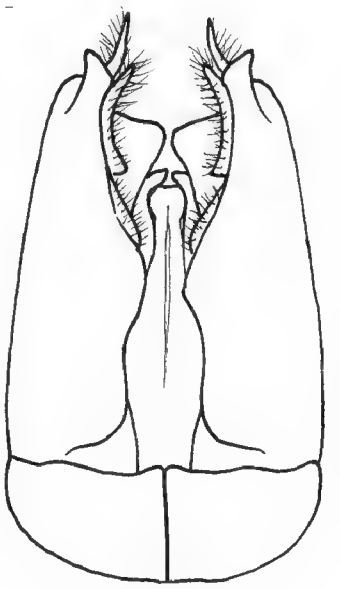
54. *D. alpicola*



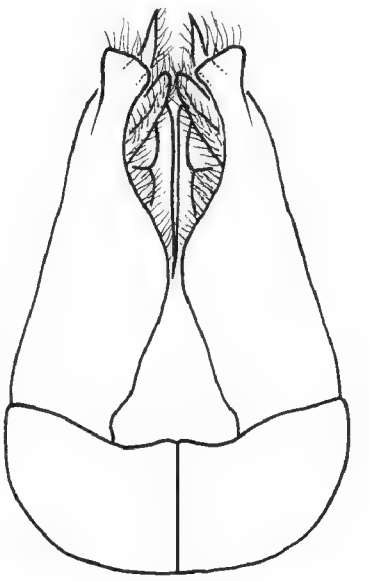
55. *D. arctica*



56. *D. arenaria*

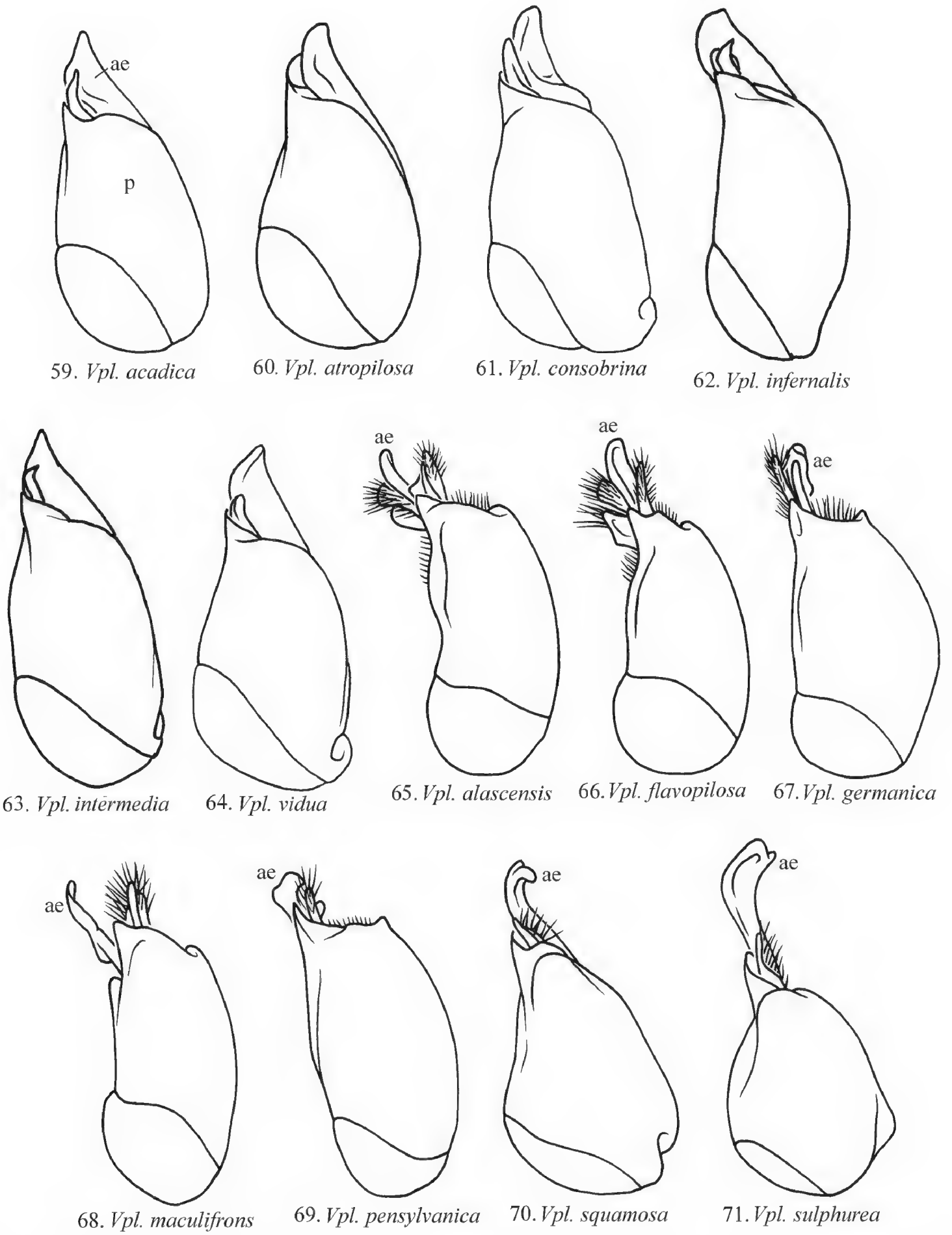


57. *D. maculata*

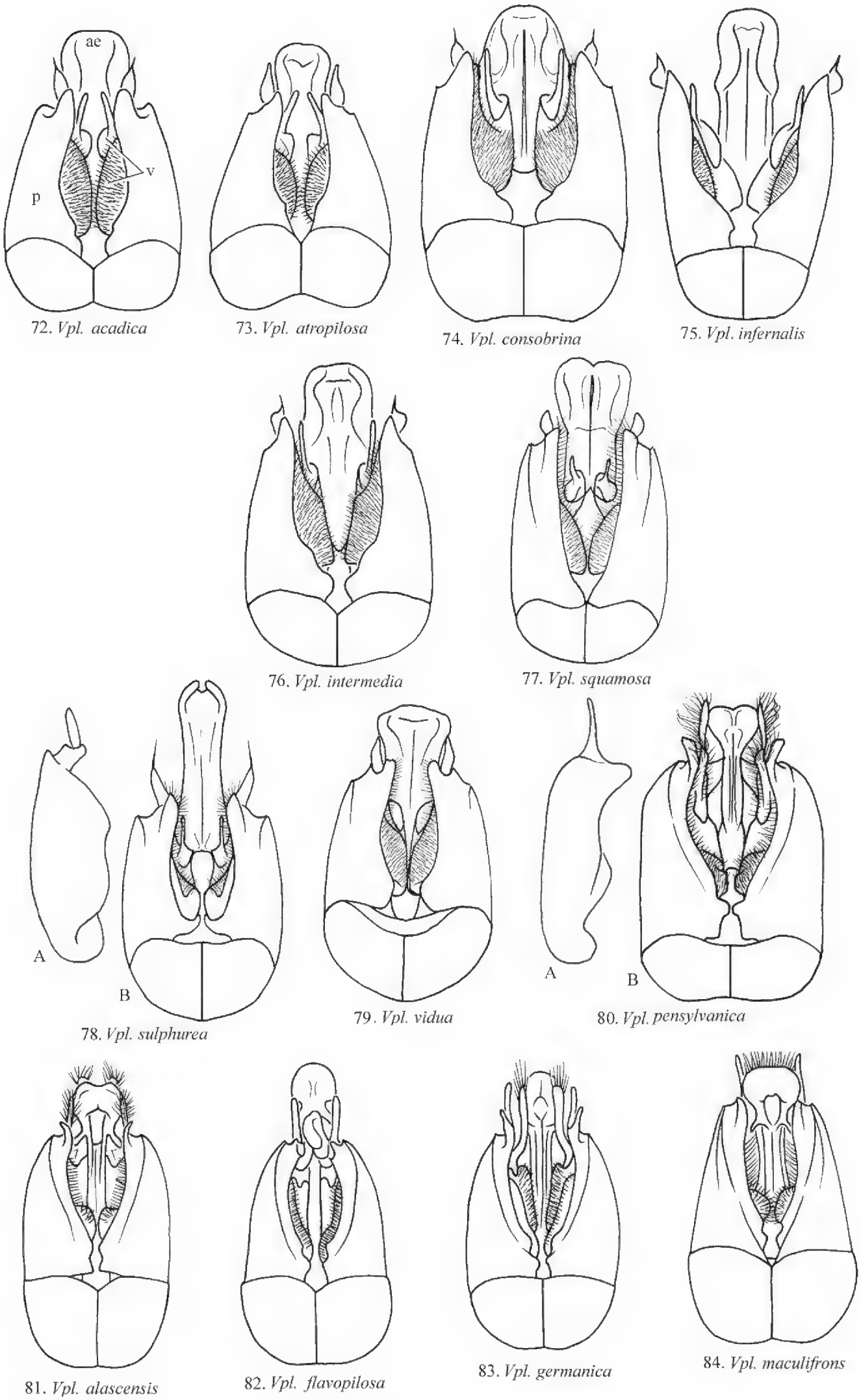


58. *D. norvegicoides*

Figures 48–58. Lateral view of genital capsule in *Dolichovespula* (*D.*) **54–58** Ventral view of genital capsule.



Figures 59–71. Lateral view of genital capsule in *Vespula* (*Vpl*). Abbreviations: **ae** = aedeagus **p** = paramere.



72. *Vpl. acadica*
73. *Vpl. atropilosa*
74. *Vpl. consobrina*
75. *Vpl. infernalis*
76. *Vpl. intermedia*
77. *Vpl. squamosa*
78. *Vpl. sulphurea*
79. *Vpl. vidua*
80. *Vpl. pensylvanica*
81. *Vpl. alascensis*
82. *Vpl. flavopilosa*
83. *Vpl. germanica*
84. *Vpl. maculifrons*

Figures 72–84. Ventral view of genital capsule in *Vespula* (*Vpl*). Abbreviations: **A.** = dorsal view of paramere **ae** = aedeagus **p** = paramere **v** = volsella **Vpl.** = *Vespula.*

Vespula maculifrons **(du Buysson)**
http://species-id.net/wiki/Vespula_maculifrons
Figs 12, 22, 43, 68, 84

Vespa maculifrons "S." Harris (in Hitchcock) 1853:589. *Nomen nudum*.
Vespa communis de Saussure 1857:117. Syntype females; "America septentr." (GENEVA, PARIS). Nec *Vespa communis* von Schrank 1785.
Vespa maculifrons "H." du Buysson 1905 (1904):608, as a synonym of *Vespa communis* de Saussure 1857. Holotype female; Deleware: Wilmington" (LONDON). Available under Article 11.6.1 of the International Code of Zoological Nomenclature.
Vespa communis var. *flavida* Sladen 1918:71. Holotype female; Canada (repository unknown).

Distribution. This species is the most common *Vespula* occurring east of the 100th meridian.

Biology. It builds subterranean nests in a wide variety of situations, even in abandoned vehicles. These yellow jackets prey on live insects and are also scavengers of sources of protein and sugar.

Vespula pensylvanica **(de Saussure)**
http://species-id.net/wiki/Vespula_pensylvanica
Figs 1c, d, 10, 23, 44, 69, 80

Vespa pensylvanica de Saussure 1857:116. Lectotype female; New Mexico (GENEVA).
Vespa occidentalis Cresson 1874:100. Lectotype female; Nevada (PHILADELPHIA) Nec *Vespa occidentalis* Olivier, 1792.

Distribution. This is the most abundant pest species of *Vespula* on the West Coast and much of the interior west of North America.

Biology. Nests are usually built in cavities, which may be in the ground or in structures, such as attics, wall voids and even basements. The nests can become huge and often become perennial in warmer climates. These wasps are general scavengers, and will feed on live prey or any other source of protein or sugar including garbage. It is adventive in Hawaii.

Vespula squamosa **(Drury)**
http://species-id.net/wiki/Vespula_squamosa
Figs 25, 45, 70, 77

Vespa squamosus Drury 1773: Index to vol. I [pl. XLIII fig. 7 in Vol. 1]. Holotype female; New York (destroyed ?).

Vespa lineata Fabricius 1775:365. Type unknown; "in America".
Sphex conchacea Christ 1791:259, pl. 25 fig. 5. Type ?; "Neuiork" (destroyed).
Vespa cuneata Fabricius 1804:258. Type?; "Carolina" (COPENHAGEN).
Vespa cruciata Lepeletier 1836:514. Unjustified emendation of *Vespa cuneata* Fabricius 1804.
Vespa bistriata McFarland 1888:298. Holotype female; "North America" (PHILADELPHIA) Nec *Vespa bistriata* Fabricius 1804.
Vespa macfarlandi Lewis 1897:180. Replacement name for *Vespa bistriata* McFarland.
Vespula squamosa var. (or subsp.) *michoacana* Bequaert 1941:249. Holotype female; Mexico: Michoacan, Tancitaro (CAMBRIDGE).

Distribution. This is an eastern species, occurring east of the 100th meridian and south to Honduras.

Biology. It is a facultative social parasite of *Vespula maculifrons*. The two striped scutum is a distinctive feature of both *Vespula squamosa* and *Vespula sulphurea*. Queens of *squamosa* are quite different in color from workers and males, with their extensive orange-brown coloration, particularly on the metasoma.

***Vespula sulphurea* (de Saussure)**
http://species-id.net/wiki/Vespula_sulphurea
Figs 11, 24, 46, 71, 78

Vespa sulphurea de Saussure 1854:137. Holotype female; California (LONDON).

Distribution. *Vespula sulphurea* is abundant in mid elevation and wildland areas in western North America.

Biology. This is the yellowest of the North American species, with a two yellow-striped scutum much like that seen in *Vespula squamosa*, but *sulphurea* occurs west of the 100th meridian. They build small, subterranean nests, generally feed on live prey; in unusual circumstances they might scavenge food.

***Vespula vidua* (de Saussure)**
http://species-id.net/wiki/Vespula_vidua
Figs 47, 64, 79

Vespa vidua de Saussure 1854:136. Syntype females; "La Caroline" (PARIS).

Distribution. *Vespula vidua* occurs in the Transition and Upper Austral Zones of eastern North America.

Biology. Most nests are subterranean but *Vpl. vidua* will also build nests in hollow logs.

Acknowledgments

JMC acknowledges the support of National Science Foundation Grant DEB-0843505. The manuscript was greatly improved by comments and suggestions from Michael Archer and Bob Jacobson.

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